Impacts of Rising CO_2 Concentration on Water Use Efficiency of Woody Grassland Invaders

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Abstract—Water availability controls plant productivity and the abundance of shrubs on many rangelands. That control is mediated by factors like atmospheric CO_2 concentration that influence plant water use efficiency. Increasing CO_2 over past and projected levels elicited a similar (mesquite, *Prosopis glandulosa*; huisache, *Acacia smallii*) or possibly greater (threadleaf snakeweed, *Gutierrezia microcephala*) relative increase in intrinsic water use efficiency (photosynthesis/conductance) of shrubs that recently have proliferated on southwestern rangelands. The contribution of higher photosynthesis to the increase differed among species, however. By increasing productivity and competition for light, higher water use efficiency may favor taller woody plants over grasses on some rangelands. Rising CO_2 may benefit shrubs that realize much of the increase in water use efficiency as higher photosynthesis.

Because plant uptake of CO_2 (carbon dioxide) through stomata unavoidably is associated with water loss, plant growth is intimately coupled to water use. It is not surprising, therefore, that the distribution (Stephenson 1990; Whittaker 1975; Woodward 1987) and productivities of woody and other species (Rosenzweig 1968; Sala and others 1988; Webb and others 1978) often are strongly correlated with water availability and soil water balance. On grasslands and savannas where plant productivity is particularly closely coupled to precipitation (Pandey and Singh 1992; Sala and others 1988; Webb and others 1978), water availability in space and time exerts a dominant climatic control on the balance between grasses and woody species (Polley and others 1996). Water availability in these systems and other arid regions may be especially important during the critical period of woody establishment when seedlings often succumb to dehydration (Donovan and others 1993; Harrington 1991; Williams and Hobbs 1989).

Important to plant performance in arid and seasonally-dry environments is the efficiency with which water is used during growth. In water-limited systems, an increase in water use efficiency resulting from the global rise in atmospheric CO_2 concentration or other factors should increase plant productivity and may contribute to changes in the species and growth form composition of vegetation by favoring taller woody plants at the expense of grasses (Polley and others 1996). Changes caused by rising CO_2 in the coupling of vegetation and climate have, however, largely been overlooked in discussions of vegetation change in these systems. Most prior treatments of species change on arid and seasonally-dry grasslands implicate climate change, fire suppresion, and overgrazing or other effects of livestock (Archer 1994; Bahre and Shelton 1993; Grover and Musick 1990; Neilson 1986).

Atmospheric CO_2 concentration has increased 25% to 30% during the last two centuries from the preindustrial level of 270 to 280 μmol CO_2/mol air (parts per million, mole fraction basis) to the current 350 μmol/mol (Neftel and others 1985; Raynaud and Barnola 1985) and perhaps 100% since the last ice age 18,000 to 20,000 years ago (Delmas and others 1980; Neftel and others 1988). Recent changes largely reflect fossil fuel combustion and accelerated changes in land use. These changes are projected to contribute to atmospheric CO_2 levels during the next century that are at least double those of the preindustrial period.

We report effects of experimentally increasing CO_2 from near Ice Age levels to the current concentration and from the current concentration to levels possible in the future on a measure of water use efficiency of seedlings of woody species that recently have increased in abundance on grazing lands in the southwestern U.S. We studied these effects on the legumes honey mesquite (*Prosopis glandulosa*) and huisache (*Acacia smallii*) and half-shrub threadleaf snakeweed (*Gutierrezia microcephala*) using stable carbon isotope signatures of leaves and leaf gas exchange measurements. Each of the species possesses the C_3 photosynthetic pathway.

Threadleaf snakeweed is found in western Texas, New Mexico, Arizona, Utah, and northern Mexico (Pieper and McDaniel 1990). This short-lived half-shrub and the morphologically-similar broom snakeweed (*G. sarothrae*) were present on rangelands 100 years ago, but increased in number following droughts in the 1950s, 1970s, and 1980s. Abundance of mesquite on southwestern rangelands has increased greatly during the last 150 years. The increase reflects expansion of the legume within its historical range or an increase in the stature and visibility of suppressed populations (Bogusch 1952; Johnston 1963). Huisache is a aggressive invader of rangeland in southern Texas and

northern Mexico. Vegetation surveys of Texas, for example, indicate an increase in the woody legume of over 20% per decade or 48% during the interval from 1964 to 1982 (USDA 1985).

Theory

Water use efficiency often is assessed at the leaf level as transpiration efficiency, the ratio of net photosynthesis or assimilation (A) to transpiration (E). In most C_3 plants, A usually is positively related to leaf intercellular CO_2 concentration (ci) over the physiological range and thus depends both on external CO_2 concentration (ca) and on the rate at which CO_2 diffuses through stomata into leaves as:

$$A = \frac{(ca-ci)g}{1.6} \qquad (1)$$

where g is stomatal (leaf) conductance to water vapor and 1.6 is the ratio of the diffusivities of water vapor and CO_2 in air. Transpiration also is regulated by g and by v, the mole fraction water vapor gradient from leaves to bulk air as,

$$E = vg \qquad (2)$$

Instantaneous water use efficiency, A/E, and the closely-related intrinsic water use efficiency, A/g $(A/E$ calculated without v), thus are directly affected by changes in both A and g, each of which is sensitive to atmospheric CO_2 concentration.

On combination and rearrangement of eq. 1 and 2, it becomes evident that A/E and A/g are positively related to ca and negatively related to ci/ca, the latter of which reflects the balance between the supply of CO_2 to the leaf and consumption of CO_2 in photosynthesis,

$$\frac{A}{E} = \frac{1}{v} \times \frac{A}{g} = \frac{1}{v} \times \frac{ca(1-ci/ca)}{1.6} \qquad (3)$$

A temporally-integrated measure of ci/ca conveniently is reflected in the difference between the stable C isotope (^{13}C, ^{12}C) compositions of photosynthesizing leaves of C_3 plants and the CO_2 present in the air in which leaves were grown (Farquhar and others 1982). Carbon fixed by plants is enriched in ^{12}C relative to the CO_2 in air and thus reflects a positive discrimination (Δ) against the heavier ^{13}C isotope where:

$$\Delta = \frac{\delta_a - \delta_p}{1 + \delta_p} \qquad (4)$$

and δ_p and δ_a are the carbon isotope compositions of plant tissues and CO_2 in air expressed in "delta" units (per mil, ‰) relative to a standard. Carbon isotope discrimination by C_3 plants can be positively related to ci/ca by

$$\Delta = a + (b-a)ci/ca \qquad (5)$$

where a and b are treated as constants that describe isotopic fractionation resulting from the diffusion of CO_2 in air and during carboxylation, respectively (Farquhar and others 1982).

Effects of Rising CO_2 Concentration on Intrinsic Water Use Efficiency___

Measurements of CO_2 concentration and of the stable C isotope compositions of air and leaves were used to calculate ci/ca (eq. 5) and intrinsic water use efficiency, A/g, (eq. 3) of seedlings of honey mesquite, threadleaf snakeweed, and huisache that were grown in atmospheres with different CO_2 concentrations. Threadleaf snakeweed and the legume mesquite were grown in separate experiments over a continuous daytime gradient in atmospheric CO_2 concentration that ranged from near that of the last glaciation (200 μmol/mol) to the present level (350 μmol/mol). Plants were grown within an elongated controlled-environment chamber located within a ventilated glasshouse (Mayeux and others 1993). Aerial parts of plants were enclosed in a tunnel-like polyethylene cover attached to the top of a 0.76 m (30 inch) deep, 0.45 m (18 inch) wide, and 38 m (125 foot) long soil container. Air was moved unidirectionally through the chamber. The dewpoint and dry-bulb temperatures of air were automatically reset to conditions within the glasshouse at five equally-spaced points along the chamber. Huisache was grown in a separate experiment at nominal CO_2 levels of 350, 700, and 1,000 ppm in air-conditioned glasshouse bays. Water was added weekly during all experiments to bring soils to field capacity.

The $\delta^{13}C$ values of air and of leaves of mesquite, snakeweed, and the concurrently-grown C_4 grass maize (Zea mays) increased linearly (became more enriched in ^{13}C) as plants depleted CO_2 from the present concentration to atmospheric levels near those of the last glaciation (figs. 1, 2). The difference between the $\delta^{13}C$ values of atmospheric CO_2 and
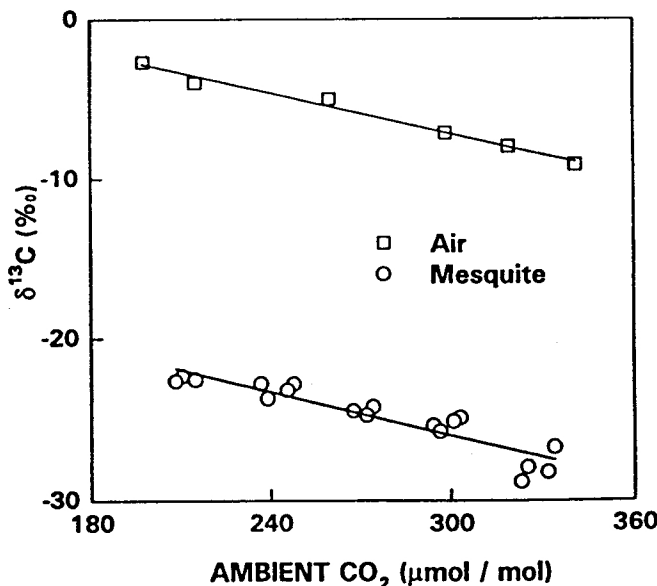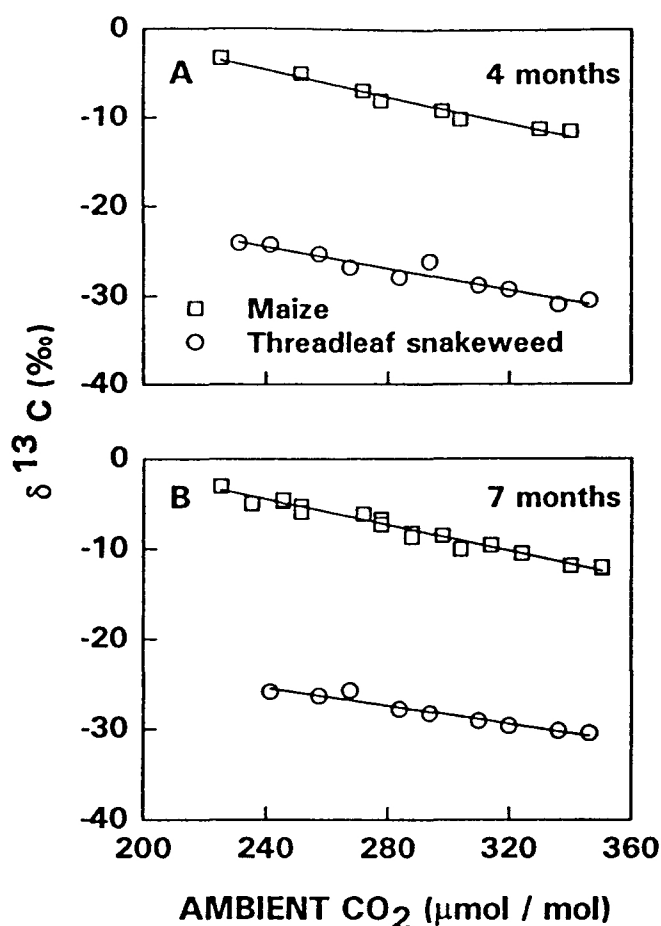

Figure 1—The stable carbon isotope composition ($\delta^{13}C$) of air and upper leaves from 1-year-old mesquite plants grown along a daytime gradient of subambient CO_2 concentration. Lines are linear regressions of $\delta^{13}C$ on instantaneous (air) or mean daytime CO_2 concentration (leaves). The figure is reproduced from Polley and others (1994).

Figure 2—The stable carbon isotope composition (δ^{13}C) of upper leaves from C$_3$ threadleaf snakeweed and C$_4$ maize plants grown along a daytime gradient of subambient CO$_2$ concentration. Snakeweed had been grown at the different CO$_2$ concentrations for (A) 4 and (B) 7 months when samples were collected. Data points for maize represent single measurements per plant. A single measurement at each CO$_2$ level was taken on a composite of leaves collected from five to six plants of 4-month-old threadleaf snakeweed (A). Values for 7-month-old snakeweed are means of δ^{13}C measurements on leaves from each of six plants per CO$_2$ level (B). Lines are linear regressions of δ^{13}C on mean daytime CO$_2$ concentration. Slopes of linear regressions differed significantly between maize and 4-($P<0.05$) and 7-month-old plants of threadleaf snakeweed ($P<0.001$).

leaf carbon of maize was found be conservative at 3.1‰ (Polley and others 1993), allowing us to use the δ^{13}C value of maize leaves grown in the same air as shrubs to calculate the isotope composition of air along the CO$_2$ gradient. Slopes of linear regressions of δ^{13}C on CO$_2$ concentration did not differ significantly between the air and leaves from 1-year-old mesquite plants (fig. 1; $P > 0.50$). As a result, Δ (eq. 4) and c_i/c_a (eq. 5) remained nearly constant across CO$_2$ concent rations, and A/g of mesquite increased by about the same relative amount as did CO$_2$ concentration (fig. 3).

Leaf δ^{13}C increased slightly more rapidly in maize than in 4- and 7-month-old plants of threadleaf snakeweed as CO$_2$ was depleted below the current concentration (fig. 2). Assuming that Δ of well-watered maize remained constant across CO$_2$ levels at 3.1‰, Δ of the shrub decreased from about 23.7 to 22.1‰ and from 24.6 to 22.3‰ as CO$_2$ rose from about 240 to 345 μmol/mol, in 4- and 7-month-old plants, respectively. The decline in carbon isotope discrimination of snakeweed as CO$_2$ increased suggests that c_i/c_a also declined at higher CO$_2$ concentrations (eq. 5), and that leaf A/g of the shrub rose by a greater relative amount than did CO$_2$ concentration (about 98% and 125% in 4- and 7-month-old plants with the 44% increase in CO$_2$ concentration from 240 to 345 μmol/mol).

Temporally-integrated values of c_i/c_a for huisache were calculated from the carbon isotope signatures of huisache and maize leaves grown at the current and elevated CO$_2$ concentrations. The c_i/c_a of 8-month-old huisache seedlings differed little among CO$_2$ treatments (mean = 0.66, 0.69, 0.71 for plants grown near 360, 700, and 1000 μmol/mol), indicating that as CO$_2$ increased, leaf A/g of the legume increased by a similar relative amount.

Instantaneous measurements of leaf gas exchange confirmed that A/g of the two legumes, mesquite and huisache, increased by a similar relative amount as did CO$_2$ concentration. In neither species did c_i/c_a vary with CO$_2$ treatment (mean = 0.65 for mesquite, n = 17; 0.74 for huisache, n = 72). Contrary to results from isotope analyses, however, gas exchange measurements on leaves and photosynthetic stems of threadleaf snakeweed indicated that c_i increased linearly and proportionally (by the same ratio) with ambient CO$_2$ (fig. 4). The c_i/c_a calculated from gas exchange measurements also did not differ with tissue type (mean = 0.87).
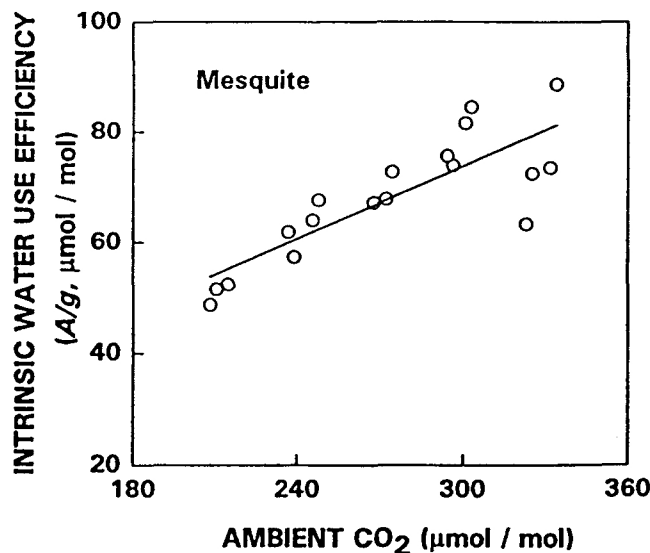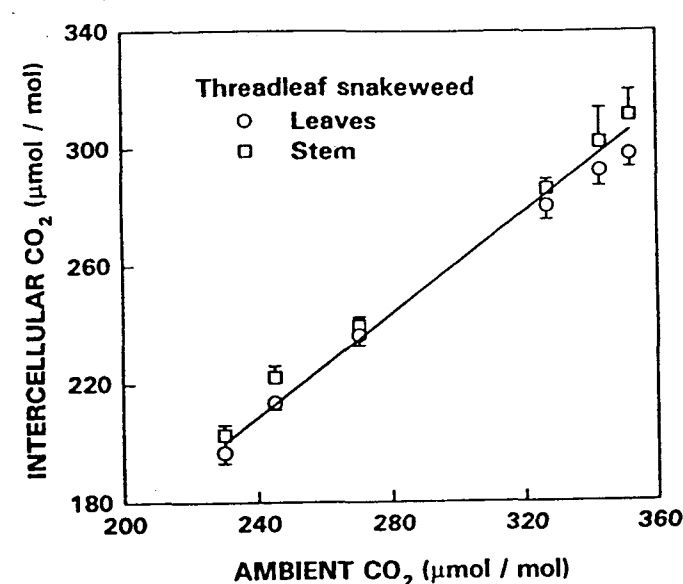

Figure 3—Relationship betwen intrinsic water use efficiency (net photosynthesis (A)/stomatal conductance to water (g)) of mesquite plants derived from the δ^{13}C of leaves and the daytime CO$_2$ concentration at which plants were grown. The line is a linear regression of A/g on CO$_2$ concentration.

Figure 4—Intercellular CO_2 concentration (c_i) of leaves and photosynthetic stems of threadleaf snakeweed plants as a function of the CO_2 concentration at which plants were grown and measured. Vertical bars denote 1 standard error of the mean of three gas exchange measurements per CO_2 level. The line is a linear regression that was fit through the origin to all data.
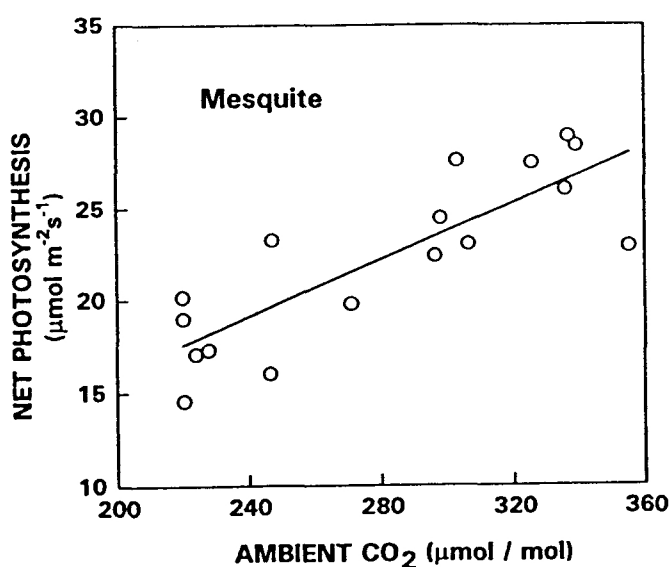
Figure 5—Leaf net photosynthetic rates of mesquite as a function of the CO_2 concentration at which plants were grown and measured. The line is a linear regression of single measurements per plant on CO_2 concentration. The figure is reproduced from Polley and others (1994).

Effects of Rising CO_2 on Net Photosynthesis and Stomatal Conductance

Gas exchange measurements also provided an indication of the extent to which changes in g and A contributed to higher water use efficiency as CO_2 rose. It was in this respect that species differed most markedly. Stomatal conductance measured at high light was not significantly altered by CO_2 from 225 to 345 µmol/mol in mesquite (Polley and others 1994). Net photosynthesis of this legume, however, increased linearly by about the same relative amount as did CO_2 concentration (fig. 5). Higher photosynthesis consequently accounted for all of the CO_2-mediated increase in A/g in mesquite. By contrast, the response of net photosynthesis to CO_2 in both leaves and photosynthetic stems of threadleaf snakeweed was strongly curvilinear (fig. 6). Photosynthesis increased markedly from about 230 µmol/mol CO_2 to near the preindustrial level of 275 µmol/mol (74 to 133%), but changed little as CO_2 was raised to the current concentration. In this species, much of any increase in water use efficiency during the last two centuries may therefore have resulted largely from a decline in conductance.

Both greater photosynthesis and lower stomatal conductance contributed to the increase in A/g of huisache from 350 to 1000 µmol/mol. Leaf net photosynthesis of huisache was not significantly ($P > 0.05$) greater in plants grown for a year near 700 µmol/mol than in those grown at 350 µmol/mol (fig. 7), but was stimulated by a further increase in CO_2 to
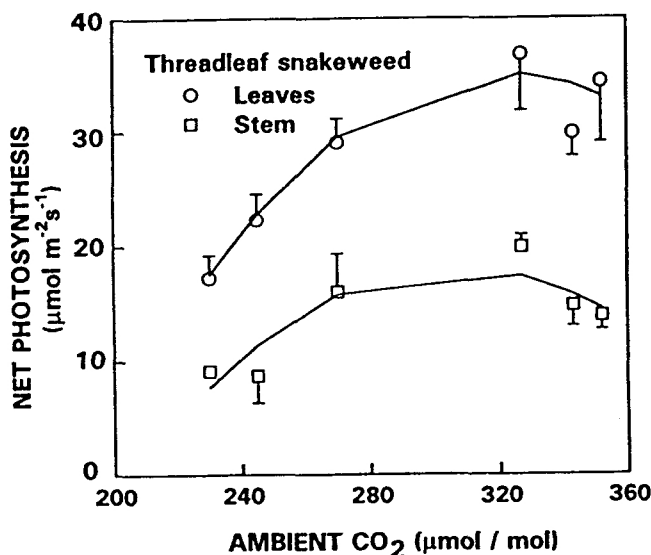

Figure 6—Net photosynthetic rates of leaves and photosynthetic stems of threadleaf snakeweed as a function of the CO_2 concentration at which plants were grown and measured. Vertical bars denote 1 standard error of the mean of three measurements on each tissue type per CO_2 level. Cubic polynomial regressions were fit to measurements on each tissue type.
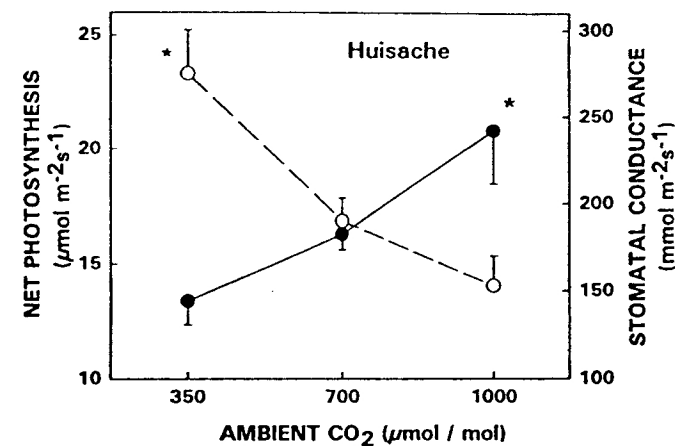
Figure 7—Leaf net photosynthesis (closed symbols and solid line) and stomatal conductance to water vapor (open symbols and broken line) of huisache measured near the CO_2 concentration that prevailed during growth. Vertical bars denote 1 standard error of the mean (n = 26, 25, and 18 leaves at 350, 700, and 1000 μmol/mol, respectively). Within measurement type, means differed significantly ($P < 0.05$) if labelled with an asterisk.

1000 μmol/mol. Conversely, stomatal conductance declined significantly from 350 to 700 μmol/mol, but did not differ at 700 and 1000 μmol/mol.

Rising CO_2, Water Use Efficiency, and Vegetation Dynamics

Increasing CO_2 dramatically increased potential water use efficiency of three shrubs that recently have become more abundant on rangelands in the southwestern U.S. A given relative increase in CO_2 concentration between 200 and 1000 μmol/mol elicited a similar (mesquite, huisache) or possibly even greater (threadleaf snakeweed) relative increase in potential water use efficiency of the shrubs. If manifested in nature, an increase in water use efficiency of the magnitude suggested during the last two centuries alone likely has increased primary productivity in water-limited ecosystems. The increase in water use efficiency may also have contributed to vegetation change. On average, for example, A/g of mesquite increased about 16.5 μmol CO_2/(mol water) with the increase in CO_2 from 275 to 350 μmol/mol that has occurred during the last two centuries. That increase is similar in magnitude to the approximately 22 μmol/mol increase in A/g that was associated with a change in C_3 composition along a soil moisture gradient in the Sonoran desert (Ehleringer and Cooper 1988). Importantly, data from huisache suggest that proportional effects of CO_2 on water use efficiency should continue unabatted to CO_2 concentrations exceeding those forecast for the foreseeable future. These changes almost certainly have contributed and will continue to contribute to species change on arid and semiarid rangelands by altering competitive relations among species or increasing plant survival during drought.

Given the differing contributions of increased photosynthesis versus decreased conductance to higher A/g that were observed among species and over different CO_2 concentrations, it is unlikely that the three shrubs would be favored similarly by a given increase in water use efficiency. Higher water use efficiency that derives primarily from lower g and transpiration may not always be competitively advantageous in water-limited environments (Cohen 1970; Delucia and Heckathorn 1989; DeLucia and Schlesinger 1991). Water that is not used by one plant may be lost to competing vegetation, evaporation, or drainage through the soil profile. Potential water savings resulting from lower g can be reduced if leaf temperature or the leaf-to-air vapor pressure gradient increase because energy is dissipated more slowly by transpiration. Further, when water is available, little or no benefit of higher CO_2 may accrue to the growth of plants that derive most of their increase in water use efficiency from a decrease in g and transpiration (Gifford and Morison 1985).

It appears from studies within and among species at the current CO_2 concentration that the opposite strategy of rapid photosynthesis and growth may be more conducive to seedling survival in a competitive environment when water is limited (DeLucia and Heckathorn 1989; Donovan and Ehleringer 1994; Donovan and others 1993). By virtue of more extensive or deeply-placed root systems, for example, larger seedlings are more competitive for surficial soil water and better able to access moisture in deeper soil layers. The greatest benefit of an increase in water use efficiency as CO_2 rises may accrue over concentrations where photosynthesis is most sensitive to CO_2 or to species which realize most of the increase as higher photosynthetic rates. We suggest, therefore, that species differences in the sensitivity of g and A to CO_2 may prove important in understanding likely consequences of an increase in water use efficiency to the success of woody and other seedlings on arid and semiarid rangelands.

Acknowledgments

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